Three new Miocene fungal palynomorphs from the Brassington Formation, Derbyshire, UK

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The Middle to Late Miocene Brassington Formation from the Peak District in Derbyshire, central UK, has yielded a diverse vegetation assemblage, but until now there have been no reports of fungal remains. Here we describe three new species of fossil fungal palynomorphs from the Kenslow Member of the Brassington Formation. The taxa have been assigned to the Chaetosphaeriaceae and Pyrenulales, respectively, and were most likely saprophytic members of the community. The extant living relatives of the new fossil fungi are commonly found on decaying wood, often submerged in freshwater. A saprobic ecology on submerged decaying wood is consistent with sedimentological evidence that shows the Kenslow Member was deposited in a lacustrine or wetland environment. This is the first reported occurrence of the genera *Rhexoampullifera* in the fossil record.

Keywords: Brassington Formation; fossil *Chaetosphaeria*; fossil *Rhexoampulifera*; fungal spores; Miocene; non-pollen palynomorphs; taxonomy; United Kingdom

1. Introduction

The Brassington Formation of central England (Fig. 1) is the most extensive onshore terrestrial Miocene deposit in the UK (Boulter et al., 1971; Walsh et al., 2018). The formation is subdivided twice into the Kirkham, Bees Nest and Kenslow members (Fig. 1; Boulter et al., 1971). The Kirkham Member is predominantly unconsolidated and semi-consolidated sand with occasional pebble layers and is unfossiliferous (Boulter et al., 1971; Walsh et al., 1972; 1980). The Bees Nest Member comprises vari-coloured clays and has also proven unfossiliferous to date, though ongoing exploration has returned samples that show promise of yielding palynomorphs (Boulter et al., 1971; Walsh et al., 1972; 1980). It is the Kenslow Member that has yielded fossil plant material (Boulter, 1971; Pound et al., 2012; Pound & Riding, 2016). Fossil wood, leaves and seeds have been reported, but represent a low diversity assemblage (Boulter & Chaloner, 1970; Boulter, 1971). The fossil pollen has not only revealed a greater diversity of plant species, but has been the only means to date the formation (Boulter, 1971; Pound et al., 2012; Pound & Riding, 2016). Recent re-analysis of the Kenslow Member has shown that its deposition was diachronous; in the Bees Nest Pit, it is Serravallian in age, whereas in the Kenslow Top Pit, it is Tortonian in age (Pound et al., 2012; Pound & Riding, 2016). This said, it retains the designation as a single member based on identical lithology and similar fossil contents in each occurrence. The pollen assemblages show that the vegetation changed from being a sub-tropical conifer dominated forest in the Serravallian to a warm-temperate mixed forest during the Tortonian (Pound & Riding, 2016). Despite the past, present and ongoing work to understand the vegetation preserved in the Kenslow Member, no research has been undertaken on the non-pollen palynomorph (NPP) component of the palynology preparations. This paper represents the first results of such study, which has, to date, concentrated on the fungal component of the NPPs. During ongoing palaeoecological study, abundant fungal remains were recovered. None of the taxa recovered to date are forms useful for constraining the age of the deposit, but are indicative of specific palaeoecological conditions present in the Brassington Formation. From these remains, we here define and describe three new fungal species. These new species are then used to further refine the palaeoenvironmental interpretation of the Kenslow Member.

2. Materials and methods

The samples came from the type section at Bees Nest Pit (53.09°N, 1.64°W) on Manystones Lane east of the village of Brassington, Derbyshire (Fig. 1, 2). In addition to standard sediment samples, an exceptionally large sample of fossil wood, likely a segment of trunk, was collected (Fig. 3). This trunk, like many other wood remnants in the Kenslow Member, contains insect borings and fungal damage, as well as deep cracks as a result of desiccation prior to fossilisation (Fig. 3). Clay, charcoal, and wood fragments are present in the majority of the cracks (Fig. 3). This poorly sorted material from voids in the trunk segment was extracted for palynological processing (Fig. 3). One gram of clay was processed using 10ml of 35% hydrochloric acid followed by two treatments with 40ml of 40% hydrofluoric acid. The residues were then mounted in glycerine jelly, studied with a Leica DM750 microscope, photographed with a Leica ICC50 W camera and annotated using Leica LAS version 4.8 software. Slides were analysed at 400x magnification and photomicrographs were obtained at 1000x magnification using oil-immersion objectives. Fungi were identified using modern morphological methods for identification of Hyphomycetes (Nuñez Otaño et al., 2017; Seifert et al., 2011).

3. Results

Below we describe the new taxa from the Kenslow Member of the Brassington Formation (Fig. 1). All holotypes and paratypes are stored in the collections of the British Geological Survey, Keyworth, Nottingham, UK. Each specimen has been assigned a unique MPK museum accession number (MPK 14619 – MPK 14623), slide numbers and England Finder coordinates are also provided.

3.1.Comment on Nomenclatural Issues

There are four competing methods for naming fossil fungal palynomorphs; these are: 1) give it the same name as a modern fungus (e.g., *Diporotheca rhizophila*; Hillbrand et al. 2012); 2) add various suffixes & prefixes to the modern fungus name to indicate a fossil form (*Palaeo-, Palae-, Paleo-, Para-, Pro-, Proto-, Pseudo-; -ates, -inites, -ites, -nites, -onites, -opsis, -phycus, -spora, -sporites, -sporonites, -thallos*; e.g., *Hypoxylonites* sp. or *Palaeoamphisphaerella sp.*; Kalgutkar & Jansonius 2000; 3) use Saccardo Spore Groups to classify form-genera and/or modern genera into seven major morphological categories (e.g., *Monoporisporites*; Seifert et al. 2011; Jansonius

& Kalgutkar, 2000); and 4) use a lab-code designation until it can be assigned to a modern taxon (e.g., HdV 10; van Geel 1978; Miola 2012; O'Keefe & van Asperen 2017). Fungal genera are known to be long-ranging (Taylor et al. 2015), and while use of modern genera are clearly appropriate in many cases, such as those described in this work, this is not always the case. The lab-code system is accepted by many Quaternary and modern palynologists, however, it is not widely accepted by those working on geological time scales, as it essentially states, we have a taxon, we do not know what it is, so we are giving it a number, and while the intent is to eventually determine what it is, in practice, the lab-codes are used extensively as identifications. Fungal taxa are given a unique identifier via MycoBank and other databases; assigning it a separate lab number is redundant. Additionally, if fossil taxa can be assigned to a modern taxon, they must be re-assigned, as it is a violation of the Melbourne Code to use form-genera or fossil names where such assignment can be made (McNeill et al. 2012; Zhang et al. 2013). For this reason, and taking into consideration the relative evolutionary stability of many fungal clades, we have deliberately chosen to follow Nuñez Otaño et al. (2017) and use modern generic names.

3.2.Systematic palaeontology

Kingdom Fungi

Phylum ASCOMYCETES

Class *EUROTIOMYCETES*

Family Incertae Sedis

Genus *Rhexoampullifera* (M.B. Ellis) P.M. Kirk & C.M. Kirk

Rhexoampullifera stogieana sp. nov.

MycoBank MB 821979. Plate 1, figures 1-6; Plate 3, figures 1-3.

Description. Fungal conidia, (n=10) 10.9-12.7 ($\bar{x}$ = 12.1) micrometres wide and (n=10) 65-71.6 ($\bar{x}$ = 67.3) micrometres long; wall 1-2 micrometres thick (table 1). The conidium is generally straight, but may be slightly bowed. It has four cells arranged semi-symmetrically around a central septum, which is somewhat obscured by darkening of the conidial wall. The central septum is (n=7) 5.9-7.7 ($\bar{x}$ = 6.68) micrometres wide. Cells on either side of the central septum are 14-15 micrometres long, and may be cylindrical to slightly doliform. Septae on the far wall

of these cells are approximately (n=7) 5.9-7.4 ($\bar{x}$= 6.6) micrometres wide. The cells beyond these septae are shorter than the central two, approximately 3-7 micrometres long and tapers slightly to the next septum, which 5-6 micrometres thick and 6-7 micrometres wide. While the majority of the conidia is highly melanised, the apical cell is both hyaline and torn. Where present in any significant length, this apical cell flares and has a slightly "frilly" aspect, giving it a collarette-like appearance. It is 6 micrometres wide at the septum and flares to 7 micrometres at the edge. The wall thins from 2 micrometres to less than 1 micrometre at the edge. Where truncated, the polar cell may appear cup-like, with short extensions of the cell wall extending from the basal septum.

Holotype. Specimen MPK 14619, Slide BNWS 2-3 EF: K50-4

Paratype. Specimen MPK 14649, Slide BNWS 1-2 EF: R38-3

Etymology. The species name refers to the cigar-like shape of the conidia and is named after a stogie – a thin elongate type of cigar.

Location. Bees Nest Pit, Brassington, Derbyshire, UK.

Remarks and comparisons. This conidia is prone to breaking on either side of a septum, especially the middle septum. It is remarkably similar to conidia of *Sporoschisma nigroseptatum* (Goh et al., 1997), having central cells longer than the penultimate cells and hyaline polar cells and similar variations in septal thickness. The genus *Sporoschisma* contains taxa with conidia that share significant numbers of features with *Rhexoampullifera*, especially *S. phaeocentri* and *S. nigroseptatum*. By definition, conidia of *Sporoschisma* are 'phialoconidia,' meaning that they develop in a phialide (Nag Raj & Kendrick 1975); no evidence has been found for phialides in samples from Bees Nest. In *Sporoschisma*, each conidium is generally cylindrical, multi-septate, melanised, has smooth walls, and pale terminal cells that have flattened or rounded ends. They range from 20-48 μm long and 7.5-15 μm wide (Nag Raj & Kendrick 1975; Goh et al. 1997); the conidia length is longer in all specimens of *R. stogieana* encountered during this study. The cell size in *Sporoschisma* conidia is generally uniform, however both *S. uniseptatum* and *S. phaeocentri* have cells that frequently vary in size (Goh et al. 1997). Slight inflations in individual cells may occur, producing a doliform appearance, as is seen in some examples of *R. stogieana*. *S. nigroseptatum* sometimes has variations in cell size that produce a pattern of

hyaline polar cells, narrow cells, and broad cells as is seen in *R. stogieana*, but more importantly, has a broad band of dark pigmentation across each septum, largely obscuring its features (Nag Raj & Kendrick 1975, Goh et al. 1997; Seifert et al. 2011). Indeed, when using the key contained in Seifert et al. (2011), *R. stogieana* keys out as *S. nigroseptatum*, however, being nearly twice as long as *S. nigroseptatum*, on average, and given the presence of the hyaline "frilly" torn cells at either end of the conidium, which are indicative of rhexolytic abscission, we feel that this Miocene conidia is not a representative of *Sporoschisma*. *Sporoschisma* has schizolytic abcission. *R. stogieana* has similarities to conidia of *Dactylaria* (Goh & Hyde 1997). It is most like *D. lignicola* in that it is a long, narrow, conidia with 5 septae arranged more-or-less uniformly around the central septum, however, *D. lignicola* differs from our specimens in that it is narrower, lacks the thickened walls across the septae, and is uniformly hyaline. *R. stogieana* resembles *Ampulliferina*, especially unfragmented chains of two conidia of *A. persimplex*, which produce the appearance of a four-celled conidium with a darkened, thickened central septum (Sutton 1969). *A. persimplex*, however, lacks the frilly, hyaline polar cells of our specimen. *Ampulliferina* as a genus has schizolytic fragmentation, unlike *R. stogieana.* The modern genus *Rhexoampullifera* contains two taxa with similarities to *R. stogieana: R. fagi and R. moravica* (Koukol 2012; Ellis & Ellis 1985; Kirk 1982). Indeed, *R. moravica* is quite similar in that it forms cylindrical, catenate conidia with 3-4 septae, not including those as the poles, and tends to be highly melanised. In *R. moravica*, the conidia form conidial chains; the polar cells of the conidia are often much shorter than the other cells. The polar cells may be more hyaline than the rest of the conidium and may take on a slightly ragged appearance, much like those seen in *R. stogieana*. It is not unusual to see a polar cell as the terminus on one end of the conidium and a rimmed, cup-like cell on the other (Koukol 2012). Unlike any specimen of *R. stogieana* recovered to date, the terminal conidum has a rounded to pointed apex. Conidia of *Rhexoampullifera* range in size from 23-45 μm long and 4-6.5 μm wide, excepting where they have a doliform shape, in which case they may be up to 13 μm wide (Kirk 1982; Castañeda-Ruíz et al. 2001; Koukol 2012). In all cases, the conidia of modern *Rhexoampullifera* are shorter than those of *R. stogieana*. This feature and the age of the present examples together warrant erection of a new species. *R. stogieana* was most abundant in the clay scraped out of cracks in fossil wood specimens collected from the Kenslow Member as exposed in the Bees Nest Pit in 2012

and 2017 (Fig. 1, 3). As such, we propose that it was likely saprophytic on wood in freshwater alluvial settings, much like *R. moravica* (Koukol 2012).

Rhexoampullifera sufflata sp. nov.

MycoBank MB 821980. Plate 1, figure 7-12; Plate 3, figures 4-5

Description. Fungal conidia, (n=5) 58.4 to 66 ($\bar{x}$ = 61.3) micrometres long and (n=5) 13.1 – 15.6 ($\bar{x}$ = 14.5) micrometres wide at the widest point; wall ranges from (n=5) 1.6 – 0.8 ($\bar{x}$ = 1.3) micrometres thick (Table 2). Septae are broad, (n=5) 4.2-6.9 ($\bar{x}$ = 5.8) micrometres in thickness, and somewhat obscured by wall darkening across the septal area. Conidia are somewhat constricted at the septae. Conidia are less symmetrical than those of *R. stogieana* and have a pronounced doliform to globose cell on one side of the central septum. This inflated cell is longer (n=4; 21.8-19; $\bar{x}$ = 20.2 micrometres) than the slightly doliform cell (n=4; 10.2-15.7; $\bar{x}$ = 12.9 micrometres) on the other side of the septum. Conidia is strongly melanised, however the apical cells are hyaline and torn. The apical cell on the bulging half of the conidium is has a slightly "frilly" aspect, giving it a collarette-like appearance. The apical cell on the non-bulging half of the conidium is truncated and appears cup-like, with a flattened bottom and short extensions of the cell wall extending from the basal septum.

Holotype. Specimen MPK 14620; Slide 68110 EF: S68-4

Paratype. Specimen MPK 14621; Slide 68110 EF: J48-1

Etymology. The species epithet is the Latin word *sufflata*, meaning swollen or bulging.

Location. Bees Nest Pit, Brassington, Derbyshire, UK.

Remarks and comparisons. The conidia designated *R. sufflata* has some similarities with *Sporoschisma*, especially with *S. uniseptatum* and *S. phaeocentri*, whose cells frequently vary in size (Goh et al. 1997). *R. sufflata* is, however, 10 micrometers longer on average than similar species of *Sporoschisma* (Nag Raj & Kendrick 1975; Goh et al. 1997), and, like *R. stogieana*, has frilly and flattened end cells on the conidia indicative of uneven rhexolytic abcission.Conidia from modern *Rhexoampullifera* have many similarities to *R. sufflata.* All have characters consistent with uneven rhexolytic abcission (a frilly aspect to one terminal cell and a rimmed,

flattened, cup-like aspect to the other; Castañeda-Ruíz et al. 2001; Koukol 2012), and have darkenings across the septae. *R. sufflata* differs from *R. stogieana* in having a cell on one side of the medial septa that is significantly inflated. Also unlike *R. stogieana*, *R. sufflata*'s cells immediately on either side of the medial septum are asymmetrical: the inflated cell is longer than the slightly doliform cell. Conidia of *R. subglobosa* and *R. fagi* (Castañeda-Ruíz et al. 2001; Koukol 2012) often have doliform cells; indeed, *R. subglobosa* is nearly round. It is possible that *R. stogieana* and *R. sufflata* may represent end-members of a morphological series with increasing length and inflation of one cell bordering the medial septum (Plate 1, figures 9-12), however, the differences are sufficient that we feel a second species is warranted. *R. sufflata* was isolated from clay removed from cracks in fossil wood from the Bees Nest pit. Given this association and the modern association of *R. moravica* (Koukol 2012), we suggest an association with decaying wood in a freshwater alluvial environment, rather than occurrence on leaves, as is indicated for the highly doliform *R. subglobosa* (Castañeda-Ruíz et al. 2001) or for *R. fagi* (Kirk 1982).

Kingdom Fungi

Phylum ASCOMYCOTA

Class SORDARIOMYCETES

Family Chaetosphaeriaceae

Genus *Chaetosphaeria*

Chaetosphaeria elsikii sp. nov.

MycoBank MB 821981; Plate 2, figures 1-24; Plate 3, figures 6-9

Description. Pentagonal-pyramidal monocellate fungal phialospore with five germinal openings on the proximal face and an attachment scar on the distal face. The dark brown cell wall thins at the germinal openings, producing a near-annulate appearance. Wall is psilate to faintly scabrate and slightly recurved between the openings, producing a near-lobate outline of the proximal face. The proximal face is slightly domed. When viewed proximally or distally, the cell has a star shaped outline, whereas when viewed laterally it has an oval to triangular outline. The cell is 20-24µm in diameter across the proximal face; the distal pyramidal portion is nearly the same height. Cell walls are 1.5µm thick at most. A flattened area surrounding the attachment scar has a diameter of 3-4µm.

Holotype. Specimen MPK 14622; EF: L47-mid

Paratype. Specimen MPK 14623, EF L50-mid

Etymology. The specific epithet is in honour of William C. Elsik, who first described this conidium but did not validate it.

Location. Bee's Nest Clay Pit, Brassington, Derbyshire, UK.

Remarks and comparisons. This conidium is very similar to both *Angulinites psilatus* ined. and *Triangulinites staplinii* ined. described by Elsik (1992) as part of short course notes for the American Association of Stratigraphic Palynologists (AASP)-sponsored short course in Houston, TX; no type specimens were indicated in this publication although both line drawings and 35-mm slides accompany the descriptions. Elsik (1992) noted that this taxon occurs in Miocene – Recent sediments and may have been present in the Oligocene. Angular fungal conidia of this type are uncommon, and largely limited to the Hyphomycetes. This phialospore has similarities to the immature conidia of *Arthrinium pterospermum* as figured by Crous & Groenewald (2013; figure 15 D, E, & F) in its gross outline, size, wall thickness, and in having a near-annulate aperture where the conidia attached to the conidiophore (Crous & Groenewald, 2013). However, conidia of *Arthrinium pterospermum* is dorsal-ventrally flattened, while this specimen is ventrally pyramidal. A fossil form of *Arthrinium*, *Arthriniites subterraneus* ined. was described for a fusiform conidium from the upper Palaeogene-lower Neogene of Armenia, however, as the present phialospore is not fusiform, any relationship is discounted. The triangular outline apparent in an equatorial view causes it to resemble ascospores of *Zopfiella lundquistii* (Shearer & Crane 1978), especially in size, wall thickness, and apparent aperturation in this orientation. However, ascospores of *Zopfiella* are dorsal-ventrally flattened, while it is clear that this taxon is not. Some spores of the Entolomataceae (Co-David et al. 2009) have a superficial resemblance to *C. elsikii* in being psilate angular spores without bumps or ridges as ornamentation, however, *C. elsikii* has multiple apertures and is highly melanised, unlike members of the Entolomataceae. The aperturate pyramidal form of this taxon has some similarities to conidiogenous cells of *Balanopsis* (Seifert et al. 2011), however, it is much larger and more pigmented than the typically hyaline, 6-8 poroid cells of *Balanopsis.* This taxon is more similar to *Chaetosphaeria novae-zelandie* (Hughes 1965). *C. novae-zelandie* has 4-5 germ openings in the dorsal side of the pyramidal phialospore, which has a flattened area around the ventral attachment scar where it met the phialide. The present phialospore is somewhat larger than the maximum dimensions

recorded for *C. novae-zelandie*; given its size and age, we opt to erect a new species (Table 3; Hughes 1965). *C. novae-zelandie* has been isolated from decaying wood of various types submerged in freshwater lakes in New Zealand (Hughes 1965). We postulate that *C. elsikii* likely had a similar habit.

4. Discussion

The three new species are the first fossil fungal remains reported from the Brassington Formation and from the Miocene of the UK (Boulter 1971; Walsh et al. 1996; Pound et al. 2012; Pound & Riding 2016; Walsh et al. 2018). *Chaetosphaeria elsikii* belongs to the Chaetosphaeriaceae, which is one of two recognized families of the Chaetosphaeriales (Maharachchikumbura et al. 2015). The order is predominantly comprised of wood-inhabiting saprobic fungi and has a cosmopolitan biogeographical distribution (Zhang et al. 2006). Extant species of *Chaetosphaeria* are known to inhabit decaying wood submerged in freshwater (Hughes 1965), decaying and well-decayed wood exposed aerially (Sivanesan & Chang 1995; Fernández & Huhndorf 2005; Atkinson et al. 2007; Mena-Portales et al. 2015), palm petioles (Hyde et al., 1999) and angiosperm leaves (Parungao et al. 2002; Costa & Gusmão 2015). Currently, no palms have been reported from the Brassington Formation and so it is likely that *Chaetosphaeria elsikii* was saprobic on either leaf litter or decaying wood (Boulter & Chaloner 1970; Boulter 1971; Pound et al. 2012; Pound & Riding 2016). Given that it was most abundant in clay scraped from voids in the large log, we suspect the latter.

Rhexoampullifera species are widely distributed with a strong association with leaf litter and decaying wood in the tropics and temperate realms (Kirk 1982; Castañeda-Ruíz et al. 2001; Koukol 2012; Lunghini et al. 2013). They are known from laurel leaves (Kirk, 1982), myrtaceous leaves (Castañeda-Ruíz et al. 2001), and decaying hardwood (Koukol 2012). The modern association of *Rhexoampullifera* species with decaying wood and leaves, implies that *Rhexoampullifera stogiana* and *Rhexoampullifera sufflata* would have had comparable niches. The Kenslow Member has not only yielded abundant decayed wood, but also some leaves (Boulter & Chaloner 1970). Currently only gymnosperm leaves have been identified; other wood remains examined to date have been too badly degraded to identify. Pollen records show a diverse angiosperm assemblage was present during the Late Miocene (Boulter & Chaloner 1970; Pound et al. 2012), however, no Lauraceae or Myrtaceae remains have been reported to date from the Kenslow Member. Like *C. elsikii*, *R. stogiana* and *R. sufflata* are most abundant in

clays scraped from voids in the large log. Together, these lines of evidence suggest that *Rhexoampullifera stogiana* and *Rhexoampullifera sufflata* may have been saprobic on the abundant wood that has been reported (Boulter 1969; Boulter & Chaloner 1970; Pound & Riding 2016).

Based on modern species distributions, all three new taxa from the Brassington Formation were saprobic and likely inhabited the abundant decayed wood that has been recovered from the Kenslow Member (Boulter & Chaloner 1970; Pound & Riding 2016; Walsh et al. 2018). The presence of *Chaetosphaeria* strongly suggests that this wood was submerged in freshwater. The sedimentology of the Kenslow Member has been interpreted as a lacustrine or wetland environment, which is entirely compatible with the presence of saprobic fungi with a preference for submerged wood (Boulter et al. 1971; Walsh et al. 2018). Pollen-based palaeoclimate estimates for the wood-bearing Kenslow Member reconstruct a humid (though possibly seasonal) subtropical climate (Pound & Riding 2016). This warmer than modern climate may have supported a high-diversity of fungi in the mixed forests that contained *Cryptomeria anglica* – a tree whose extant relative (*Cryptomeria japonica*) reaches 40-60 m in height (Boulter 1969; Boulter & Chaloner 1970; Suzuki & Tsukahara 1987; Tsukada 1982; Pound & Riding 2016).

Chaetosphaeria has previously been reported from the fossil record as *Chaetosphaerites*, whereas *Rhexoampullifera stogiana* and *Rhexoampullifera sufflata* are the first reported occurrences of this genus in the fossil record. *Chaetosphaerites bilychnis* was named by Felix (1894) for phragmosporae that resembled *Chaetosphaeria* found in Rhamnaceae wood from the Eocene of Azerbaijan (Felix 1894; Andrews Jr. 1970). This specimen contains four cells separated by walls with equal thickness to the outer wall, the lowest cell of the specimen is triangular in outline and the upper is semi-circular (Kalgutkar & Jansonius, 2000). Other species include *Chaetosphaerites obscures* (Ke & Shi) Kalgutkar & Jansonius 2000, *Felixites pollenisimilis* (Horst 1955) Elsik 1990 and *Chaetosphaerites raoi* (Ramanujam & Rao) Kalgutkar & Jansonius 2000, which come are reported from rocks dated to the Eocene-Oligocene, Carboniferous and Miocene, respectively (Kalgutkar & Jansonius 2000). Germeraad (1979) compared a specimen from the Middle Eocene Richmond Formation of Jamaica to *Chaetosphaeria*, but this comparison was not maintained due to the hyphal structure of the Jamaican specimen (Germeraad 1979). To date, this is the first report of a phialospore of

Chaetosphaeria from the fossil record. Rhexolytic abscission, a characteristic of *Rhexoampullifera*, among other taxa, has been reported from fungal remains of the Early Eocene Princeton Chert from British Columbia, Canada (Klymiuk et al. 2013). This specimen was found as a saprobic aquatic ascomycete on remains of the enigmatic angiosperm *Eorhiza arnoldii* and compared to the extant *Xylomyces giganteus*, which is morphologically quite different from *Rhexoampullifera* (Klymiuk et al. 2013). Naming fossil fungal taxa has long since led to challenges in interpretation of paleoecology, and hampered our understanding of fungal evolution, diversity, and ecology. In the case of *Chaetosphaeria*, which not only reproduces sexually, forming a teleomorphic reproductive structure, but also asexually, producing anamorphic structures, use of modern identification methods is vital, otherwise each reproductive organ may be treated as an individual taxon, thus overinflating estimates of fungal species diversity in the past. Likewise, recognition of key characters, such as abscission scars, allows for fossil taxa to be accurately correlated with modern groups, rather than being placed in form-genera based on cell number and condition, thus resulting in underestimates of fungal richness in the fossil record. As palaeontologists build capacity to use modern mycological morphological methods, we are better able to constrain paleoenvironments. Additionally, as we are able to recognize both anamorphs and teleomorphs, we are able to define fossil holomorphs of fungi, a practice key to providing fossil evidence supporting molecular phylogenies.

The cosmopolitan nature of *Chaetosphaeria* and *Rhexoampullifera* in the present day suggests that *Chaetosphaeria elsikii*, *Rhexoampullifera stogiana* and *Rhexoampullifera sufflata* should be found in other Late Miocene wood-bearing sediments deposited in freshwater settings, although perhaps not in tropical settings (O'Keefe, 2017). Fungal palynomorphs and fungal damage to wood have been reported in coals from the Nováky and Handlová mining districts of Slovakia (O'Keefe et al. 2011) and from the Mili coal in China. Fungal hyphae have been reported in wood from the Bükkábrány fossil forest in Hungary (Erdei et al. 2009; Bardet & Pournou 2015; Nikolouli et al. 2016) and biomarkers (that may be indicative of fungi) have been extracted from North Alpine Foreland Basin and Lubstów deposit woods (Bechtel et al. 2007; 2008). Like initial research on the Brassington Formation, palynological studies of these sites have typically been focussed on the pollen and spore content to reconstruct vegetation, with fungal remains either left unidentified or subject to ongoing research (Boulter 1971; Erdei et al. 2009; Worobiec 2009; Worobiec et al. 2009; Pound & Riding 2016; Worobiec & Worobiec 2017). Continued

palynological research, with a focus on identifying fungal remains to modern genera (where possible) rather than form taxa, will elucidate the full diversity and ecology of these Miocene warmer than present forests (Utescher et al. 2007; Pound et al. 2011). As fungi are a key component of the carbon cycle, understanding the fluctuations in fungal taxonomic and functional diversity with palaeoclimate changes could provide a better understanding of past changes in atmospheric carbon dioxide concentration (Clemmensen et al. 2013; Quirk et al. 2014). This is of vital importance in the Miocene, where atmospheric carbon dioxide concentration reconstructions cannot be easily reconciled with wider palaeoclimate evidence (Knorr et al. 2011; Boyd et al. 2018).

5. Conclusions

The three new species of fungal palynomorph described from the Kenslow Member herein represent saprophytic members of the diverse forest ecosystem that grew under a warmer than present climate. The extant species of the new fossils are often associated with decaying wood in freshwater, which is consistent with sedimentological interpretations of the Kenslow Member. Identifying the Kenslow Member fungal remains to modern-affinities, rather than using form-based taxonomy, has allowed a deeper insight into the palaeoenvironment of the Brassington Formation. As such we would encourage all palynologists utilising fungi to use taxonomic assignments based on fungal affinity, rather than form-based identification whenever possible. This work is an initial step forward in our knowledge of the palaeoecology of the Brassington Formation, as well as the taxonomic and functional diversity of fungal taxa in the warmer than modern Miocene forests of Europe.

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571 Figures

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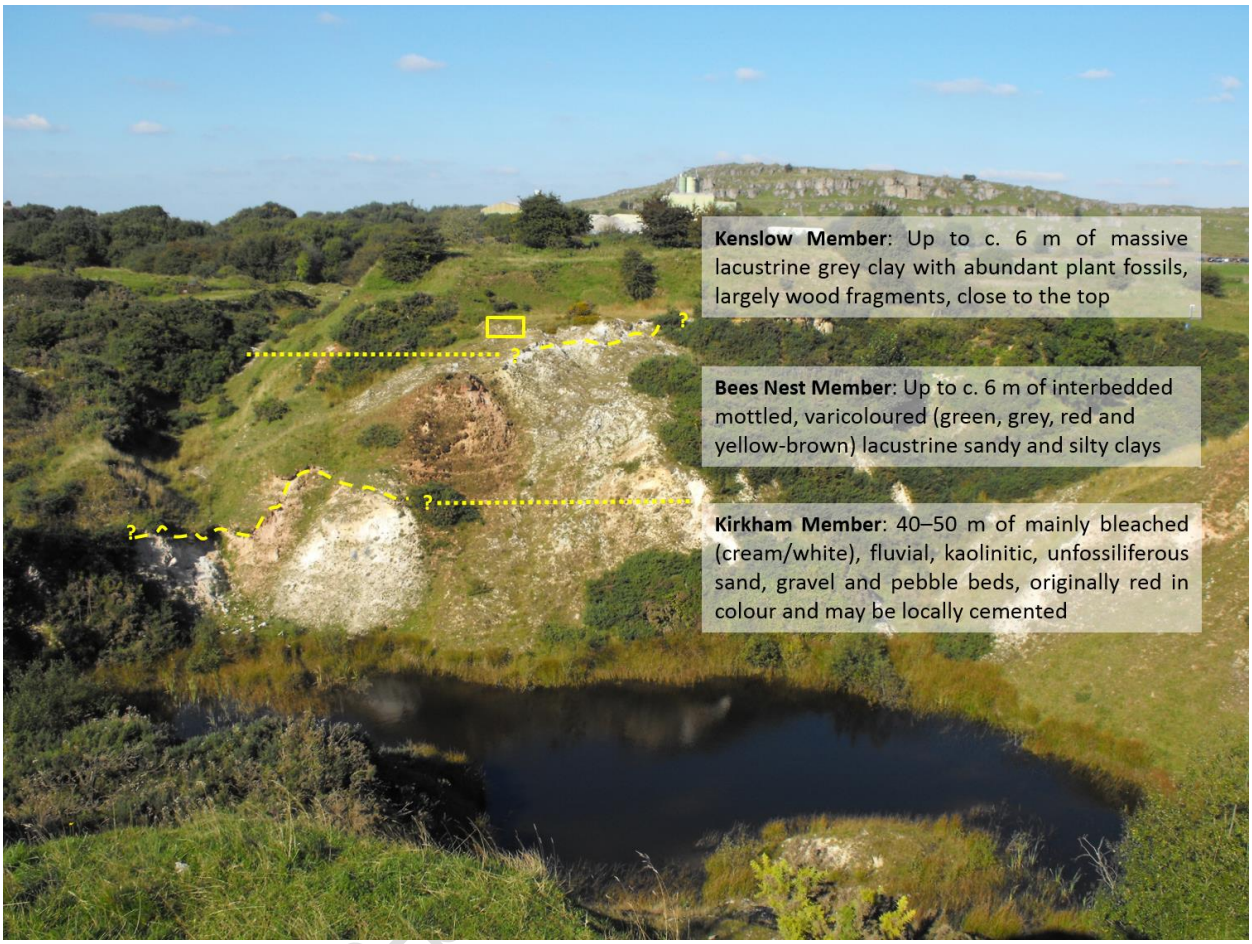

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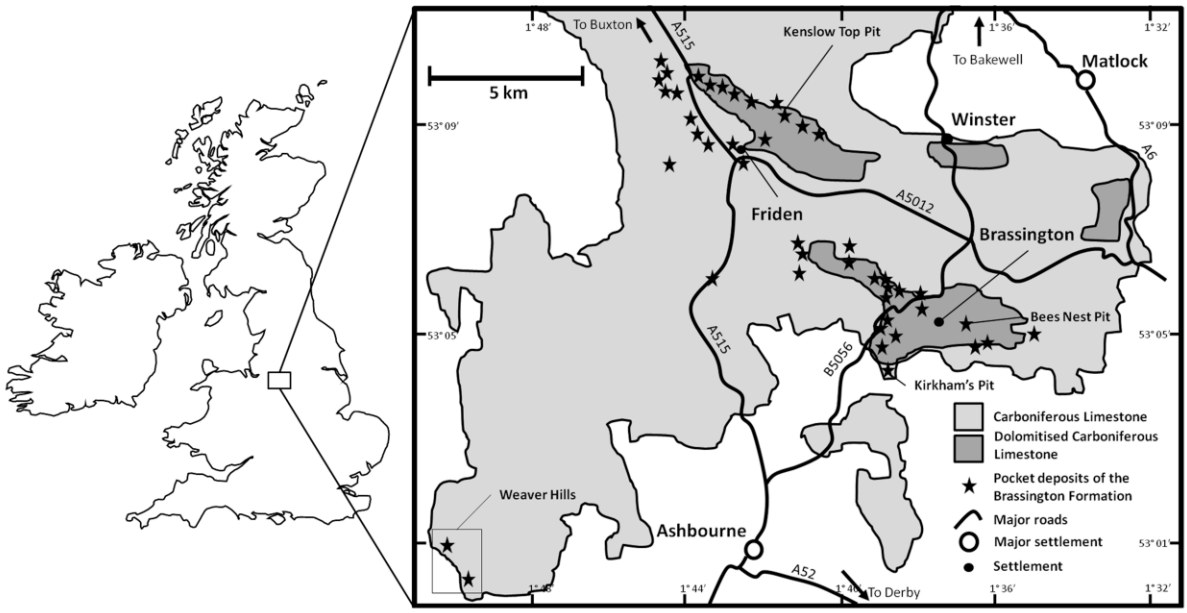
574 Figure 1. Annotated field photo of Bees Nest Pit (facing north from the south edge of the pit).
575 Harborough Rocks is the topographic high in the background with the Hoben International
576 ceramic, glass and refractory manufacturing plant juxtaposed in front of it. What remains of the
577 upper-portion of the type section (Boulter et al., 1971) is visible in this view. The yellow box
578 indicates where samples of the Kenslow Member were taken, including the wood fragment
579 (Figure 3) from which the new fungal palynomorph species are from.



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581

582 Figure 2. The location of Bees Nest Pit on the dolomitized limestone near the village of
583 Brassington, Derbyshire, central England. This map is adapted from Pound & Riding (2016) and
584 Pound et al., (2012).

585

586

587 Figure 3. Fossil wood fragment from the Kenslow Member of Bees Nest Pit. A. Photograph of
588 the whole wood fragment specimen showing the actual fossil colour (cleaned section to the
589 upper-left of the scale bar) and the location of the sediment filled crack that was sampled
590 (arrow). B. Close up view of the sediment filled crack that was sampled for palynomorphs. The
591 sediment contains abundant angular fragments of wood, charcoal and lithics in a clay matrix.
592 Total scale bar length is 13 cm (cm scale is the smaller squares).

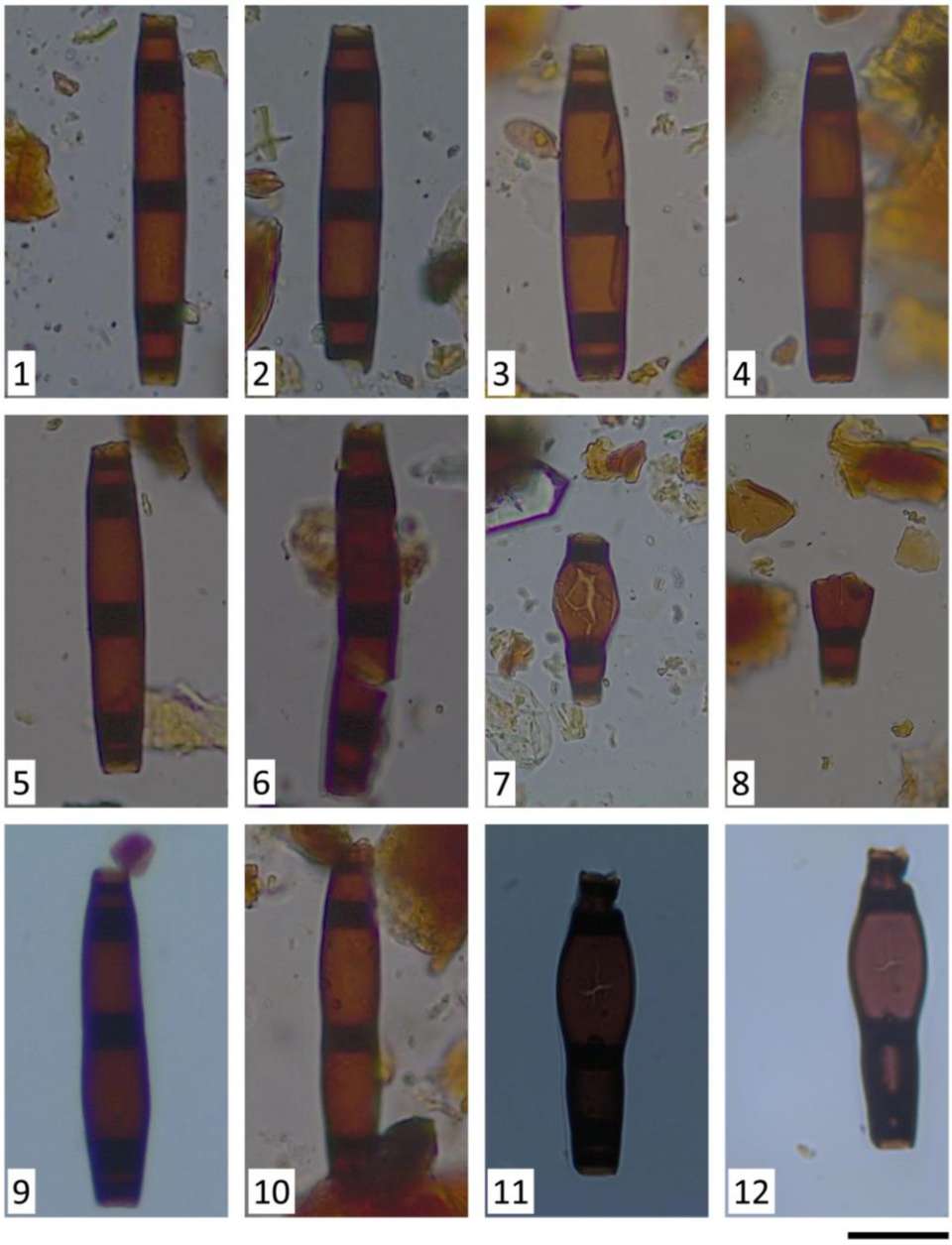


Plate 1. Photomicrographs of the newly described fungal palynomorphs from the Kenslow Member of Bees Nest Pit, Derbyshire. EF = England Finder coordinates. Figure 1. Holotype of *Rhexoampulifera stogieana*, MPK 14619, EF: K50-4 (MycoBank number: 821979). Figure 2. Paratype of *R. stogieana*, MPK 14649. Figure 7-8: Examples of broken *R. sufflatus*, showing abcission near septae. Figure 9. Paratype of *R. sufflata* MPK 14621; EF: J48-1. Figures 10-11: additional specimens of *R. sufflata*. Figure 12. Holotype of *Rhexoampulifera sufflata*, MPK 14620; EF: S68-4 (MycoBank number: 821980). Scale Bar = 20 micrometres.

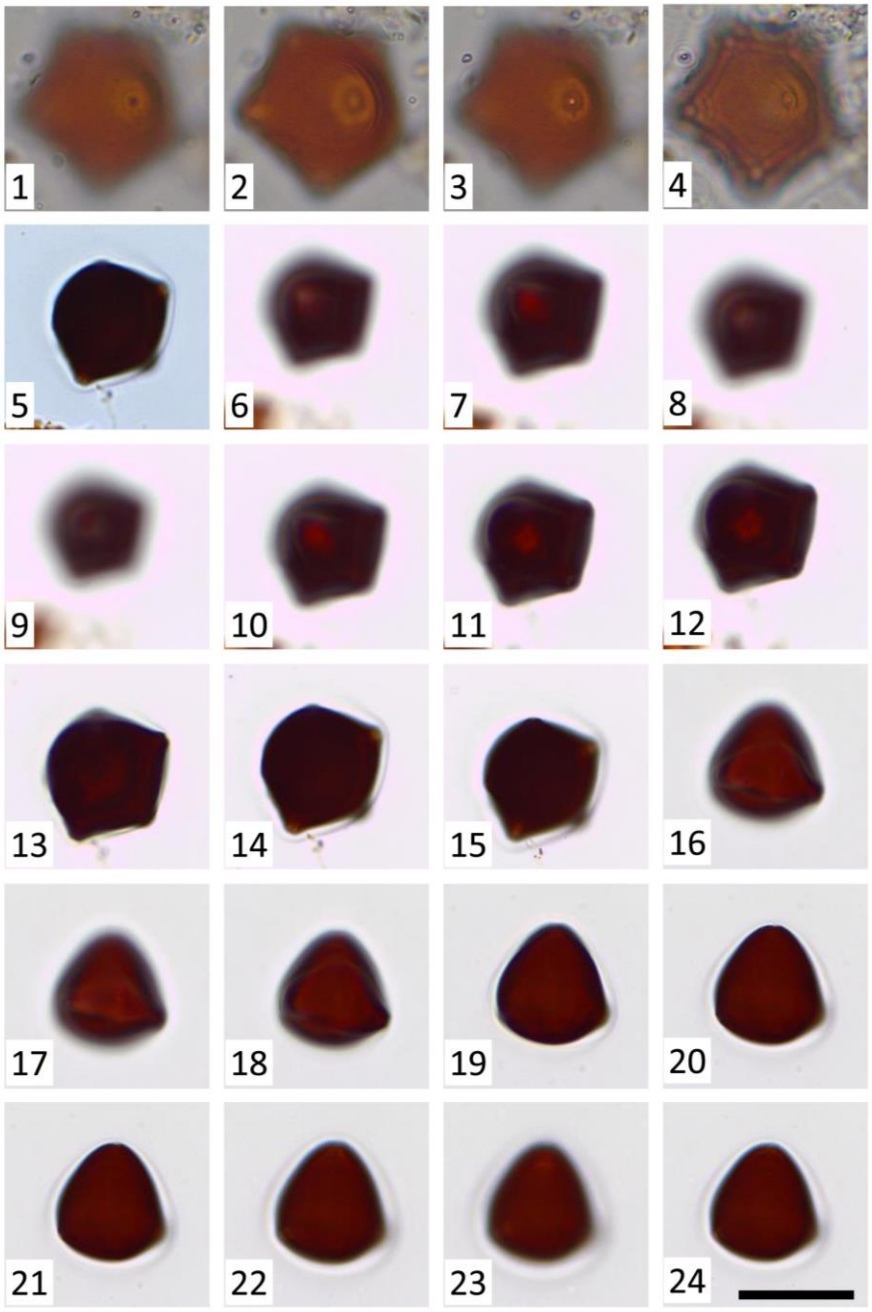
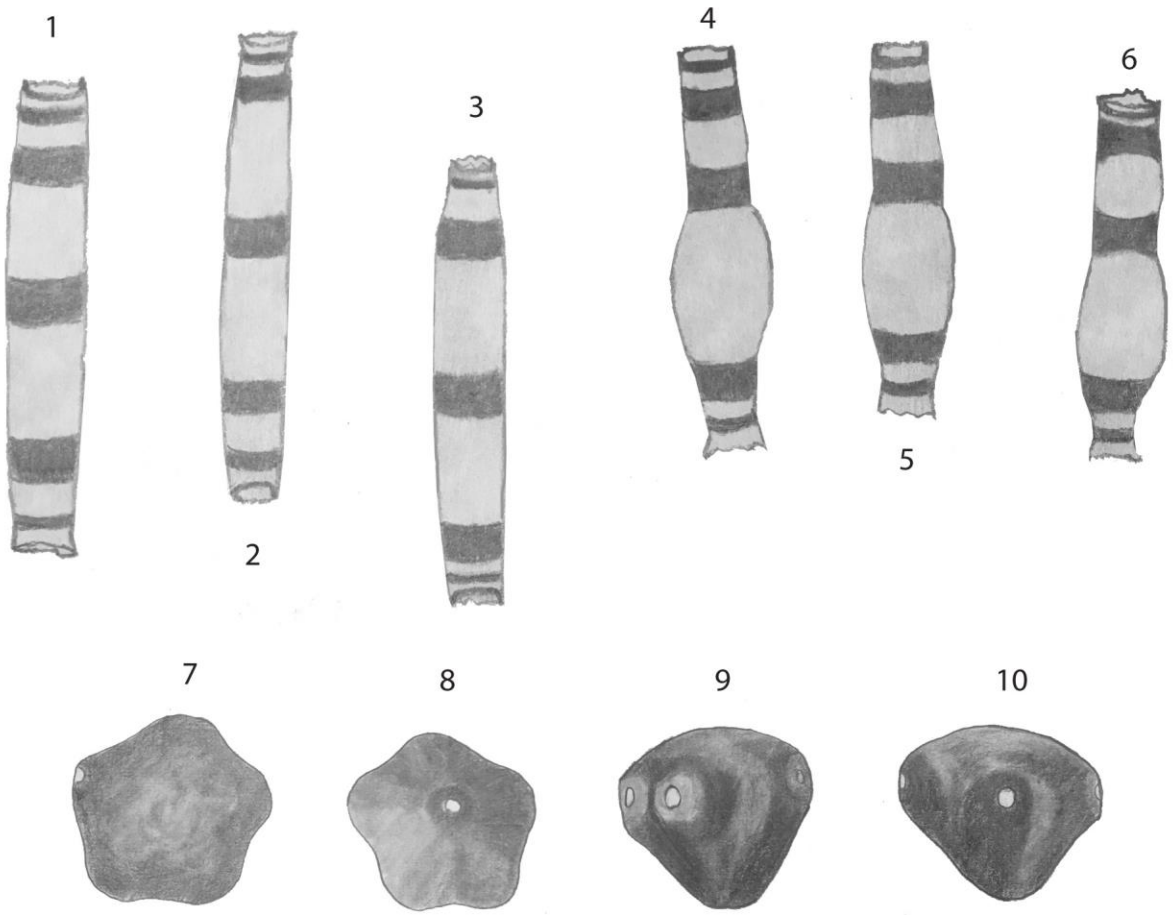


Plate 2. Figure 1-4: Holotype of *Chaetosphaeria elsikii* at varying focal levels, MPK 14622; EF: L47-mid (MycoBank number: 821981). Figure 1 is at a low focus level, graduating to a high focus level in figure 4. Figures 5-8. Paratype of *Chaetosphaeria elsikii* at varying foci levels, MPK 14623; EF: L50-mid (MycoBank number: 821982). Figure 5 is at a low focus level, graduating to a high focus level in figure 8. Figure 9-24. Additional specimens of *C. elsikii*. Scale Bar = 20 micrometres.



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609 Plate 3. Pencil sketches showing major features of *R. stogiana, R. sufflata,* and *C. elsikii*. Figure
610 1-3. Examples of *R. stogiana.* Figure 2-6. Examples of *R. sufflata.* Figure 7-10. Examples of *C.*
611 *elsikii.* Figure 7 is a top view, figure 8 is a bottom view showing the attachment scar, figures 9-
612 10 are side-views showing the conical shape of the grain and protruding apertures. Scale Bar =
613 20 micrometres.

Slide	EF Coordinates	Length	Width	L:W ratio	maximum thickness of dark band obscuring septum			End width		Wall Thickness
					septum 1	Septum 2	septum 3	End 1	End 2	
Wood Sample 1-2	Q45/1	71.6	11.8	6.1	6.6	7	6.1	9	8.3	1.8
Wood Sample 1-2	H43/mid	69.8	10.9	6.4	5.9	5.9	4.6	8.2	8.2	1.2
Wood Sample 1-2	Q43/mid	65.7	12.5	5.3	7.4	7.7	6.8	10.3	8.6	1.3
Wood Sample 1-2	R38/3	65.0	11.4	5.7	6.8	6.6	5.5	8	7.8	1.1
Wood Sample 1-2	U42/1	65.6	12.5	5.2	6.5	6.1	4.9	9.5	8.7	1.3
Wood Sample 2	H47/mid	65.0	12.7	5.1	6.1	7	6.3	10.1	7.8	1.2
Wood Sample 2	N47/4	65.7	12.3	5.3	6.6	6.5	6.7	9	7.7	1.7
JOMSUGL 907-1	J44/mid	67.6	13.5	5.0	6.7	7.2	6.6	8.8	8.0	1.9
JOMSUGL 907-1	M45/1	70.6	12.3	5.7	7.9	8.1	7.2	8.6	8.5	1.9
JOMSUGL 907-1	R48/2	74.5	14.3	5.2	8.2	8.5	7.4	8.6	8.5	1.9
Average Dimensions		**68.1**	**12.4**	**5.5**	**6.9**	**7.1**	**6.2**	**9.0**	**8.2**	**1.5**

614 Table 1. Measurements of individual Rhexoampullifera stogieana specimens and average dimensions. All measurements are in mm.

Slide	EF Coordinates	Length	Width at widest	L:W ratio	maximum dark band obscuring septum thickness	width of 2nd widest cell	width of narrow cell before hyaline cell	Wall thickness
MPA 68110	K2/2	58.4	15.3	3.8	5.5	11.2	9.0	1.3
MPA 63613	J48/1	58.5	14.9	3.9	4.2	11.1	7.9	0.8
MPA 63613	G2/mid	59.7	15.6	3.8	6.8	11.5	8.1	1.4
Wood Sample 1-2	Q38/mid	63.7	13.1	4.9	5.5	11.0	9.7	1.2
JOMSUGL 907-1	G45/1-3	66.0	13.5	4.9	6.9	11.2	9.2	1.6
Average Dimensions		**61.3**	**14.5**	**4.3**	**5.8**	**11.2**	**8.8**	**1.3**

615 Table 2. Measurements of individual Rhexoampullifera sufflata specimens and average dimensions. All measurements are in mm.

616

Slide	EF Coordinates	height	Width	Pore-pore distance	Diameter of flattened area near attachment scar	Wall thickness
MPA 63613-1	K51/3	23.2	21.3	21.2	4.0	1.3
MPA 63613-2	L23/1	23.1	20.8	21.1	3.0	1.0
MPA 63513-2	U24/4	24.4	23.9	17.1	3.8	1.4
Average Dimensions		**23.6**	**22.0**	**19.8**	**3.6**	**1.2**

Table 3. Measurements of individual Chaetosphaeria elsikii specimens and average dimensions. All measurements are in mm.